

The Bathypelagic Mysid *Gnathophausia* (Crustacea) and Its Distribution in the Eastern Pacific Ocean

LINDA HAITHCOCK PEQUEGNAT¹

A NEED HAS LONG EXISTED for an improved collecting device for capturing the larger and more actively swimming bathypelagic animals of the sea. The Isaacs-Kidd Midwater Trawl was developed at the University of California's Scripps Institution of Oceanography in 1950 and has largely satisfied this need (SIO Reference 53-3, 1953).

Bathypelagic specimens have frequently been captured in the deeper hauls of the standard one-meter plankton nets. However, the self-depressing midwater trawl, larger and capable of greater depths (up to 4000 m) and speeds (up to 5 knots) than the standard 1-meter net, has given us more productive samplings of the larger bathypelagic forms (Figs. 1 and 2). In addition, the midwater trawl has captured many species of deep-sea fishes not previously reported in the Pacific as well as species entirely new to scientific literature—forms which apparently have previously eluded capture at these depths by traditional, less effective collecting devices.

The midwater trawl collections made by the Scripps Institution of Oceanography in the eastern Pacific Ocean during the period 1950–53 were examined for the presence of the mysidacean genus *Gnathophausia*, a striking crimson red crustacean conspicuous in midwater trawl hauls from bathypelagic waters. The order Mysidacea has been divided into two subgroups based upon very widely separating morphological characteristics: the suborder Mysida and the phylogenetically more primitive suborder Lophogastrida. *Gnathophausia* is the "giant" genus in the suborder Lophogastrida, containing the largest mysids ever reported. All of the species of *Gnathophausia* are bathypelagic and

are practically never encountered in shallow water.

Specimens of *Gnathophausia* have been described from as early as the Challenger Expedition in 1873–76 (Sars, 1885 and Willemoes-Suhm, 1875), and have been reported from all parts of the world from such other pre-twentieth century expeditions as the *Talisman*, the *Albatross*, the *Oceania*, and the *Investigator*. The *Dana* Expedition in 1928–30 and the *Discovery* Expeditions in the 1920's and 1930's have revealed specimens of this genus in greater numbers and from even more widespread locations throughout the world. Prior to the *Dana* Expedition relatively few specimens of *Gnathophausia* had ever been captured—probably fewer than 100 altogether. A total of 1,051 specimens of *Gnathophausia* were taken by the *Dana*, adding considerably to our knowledge of this group of animals. The distribution and biology of *Gnathophausia* is reported in the greatest detail to date by Fage (1941) in his study of the vast *Dana* collections.

Few studies were made of bathypelagic animals in the eastern Pacific Ocean prior to the development of the midwater trawl and the subsequent collections made by the Scripps Institution during and after its development. Banner (1947) reported on one species of *Gnathophausia* (involving 24 specimens) from the northeastern Pacific off Canada and Alaska, and Banner (1954) discussed the distribution of two species of *Gnathophausia* from collections made off the California coast by the Allan Hancock Foundation. These latter collections involved fewer than 30 specimens of *Gnathophausia* and were taken from shallower levels than those sampled by the midwater trawl.

The development of the midwater trawl at the Scripps Institution has produced a rich collection of bathypelagic specimens, particularly from the eastern Pacific Ocean area. A total of 400 specimens of *Gnathophausia* were availa-

¹ Formerly with the Scripps Institution of Oceanography, University of California at La Jolla, California. Present address: c/o Department of Oceanography, Texas A & M University, College Station, Texas. Manuscript received March 23, 1964.

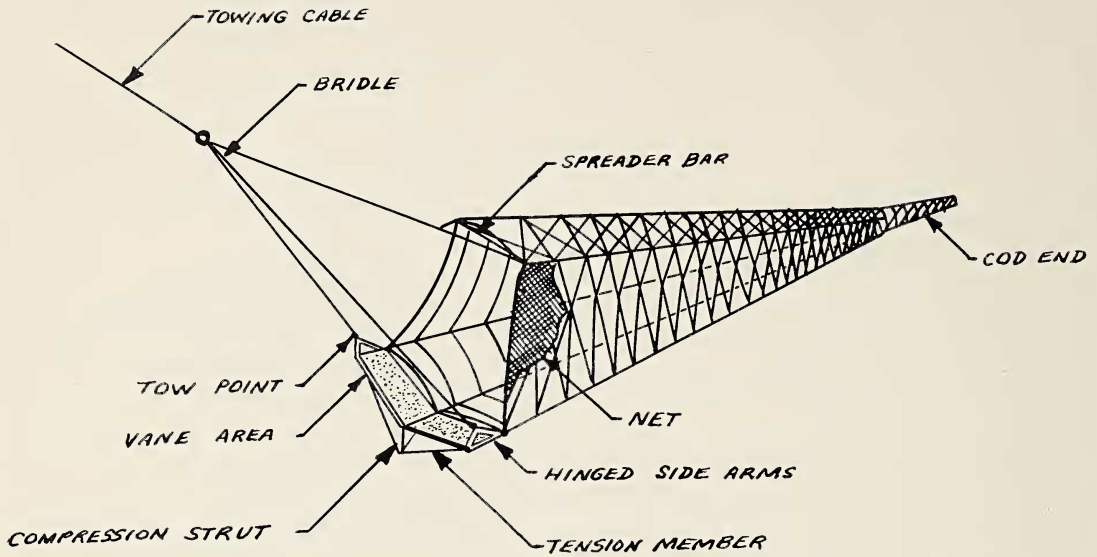


FIG. 1. The Isaacs-Kidd Midwater Trawl. (From SIO Oceanographic Equipment Report, 1953.)

ble for study from the Scripps 1950-53 collections.

In all eight species of *Gnathophausia* are recognized: *G. ingens* (Dohrn), *G. gigas* Willemoes-Suhm, *G. gracilis* W-Suhm, *G. zoea* W-Suhm, *G. elegans* G. O. Sars, *G. longispina* G. O. Sars, *G. affinis* G. O. Sars, and *G. scapularis* Ortmann. Of these eight species, four have been identified in the midwater trawl hauls from the Scripps 1950-53 collections in the eastern Pacific. They are *G. ingens*, *G. gigas*, *G. gracilis*, and *G. zoea*.

SYSTEMATIC REVIEW AND MORPHOLOGY

Since the time of Boas' early report (1883) the mysidaceans have been separated from the euphausiaceans into two distinct orders of the crustacean subclass Malacostraca. These two groups had previously been joined in the order Schizopoda (now abandoned) of Latreille (1817). Hansen (1893) and Calman (1904) further agreed with Boas in separating the two groups, allying the Euphausiacea with the Decapoda in the tribe Eucarida and allying the Mysidacea with the orders Cumacea, Tanaidacea, Isopoda, and Amphipoda in the division Peracarida. An excellent review of the historical systematics and nomenclature of the Mysidacea in relation to other crustacean groups

appears in Tattersall and Tattersall (1951), and the reader is referred to this work for the detailed and complete summary.

KEY TO SUBORDERS OF MYSIDACEA²

1. Branchiae (podobranchiae) present on some or all of the thoracic limbs. Marsupium of seven pairs of brood lamellae. Pleopods in both sexes with both rami multiarticulate and natatory; none secondarily modified in the male. No statocyst on endopod of uropod. LOPHOGASTRIDA
2. Branchiae (podobranchiae) absent. Marsupium generally of fewer than seven pairs of brood lamellae. Pleopods of male natatory or reduced, one or more pairs usually modified as accessory copulatory organs; pleopods of female reduced to simple undivided plates, not natatory. Statocyst usually present on endopod of uropod. MYSIDA

The suborder Lophogastrida, with which we are concerned in the study of *Gnathophausia*, is divided into two families: (1) the Lophogastridae containing five genera, *Lophogaster*, *Paralophogaster*, *Chalaraspidium*, *Ceratolepis*, and *Gnathophausia*; and (2) the Eucopiidae with the single genus *Eucopia*.

² From Tattersall and Tattersall, 1951.

KEY TO THE THREE MOST COMMON GENERA
OF THE SUBORDER LOPHOGASTRIDA³

1. Branchiae present on all or some of the thoracic limbs. Pleopods well developed in both sexes, natatory, unmodified. No statocyst. Marsupium with seven pairs of brood lamellae (oostegites). 2
2. Pleural plates of abdominal somites distinct and moderately well developed. 3
- 2'. No pleural plates on abdominal somites. Outer margin of scale naked. Telson entire. *Eucopia*
3. Exopod of uropod divided by a suture near the apex. Maxillules with endopod in the form of a reflexed two-segmented palp. *Gnathophausia*
- 3'. Exopod of uropod undivided; outer margin naked and ending in a tooth. Maxillules without endopod. Antennal scale heart-shaped, outer margin serrated . *Lophogaster*

*Distinguishing Characteristics of the Genus Gnathophausia*⁴

1. CARAPACE: Rather large, only loosely covering the trunk for most of its length, and exteriorly provided with raised longitudinal keels. Posterior part of carapace usually drawn out dorsally into a posteriorly pointing spine (more pronounced in younger than in mature specimens).

2. ROSTRUM: Elongated and spiniform.
3. ANTENNULE: Antennular peduncle short and thick, outer flagellum greatly produced.
4. ANTENNA: Antennal scale of somewhat varying form in different species.
5. EYES: Eyes well-developed with a small papilla issuing from the stalk anteriorly.
6. MAXILLULE: Posteriorly recurved palp on maxillule armed with long setae especially at distal end.
7. MAXILLA: Third segment has a long, well-chitinized lobe which is incised right to its

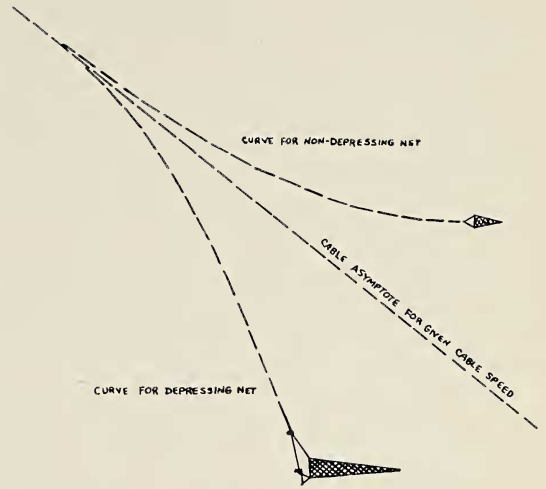


FIG. 2. Comparison of Isaacs-Kidd Midwater Trawl with non-depressing net. (From SIO Oceanographic Equipment Report, 1953.)

base forming two long, slender, finger-like processes armed with setae only at their tips. On the outer side of the coxa there is a brightly pigmented papilla which bears the opening of a gland producing a luminous secretion.

8. THORACIC LIMBS: Maxillipeds with exopodites either very small or entirely lacking. Remaining thoracic limbs nearly uniform, all provided with exopods.

9. BRANCHIAE: Those on second to seventh thoracic limbs divided into four branches with irregularly lobed pinnules. Branchiae on eighth thoracic limb rudimentary.

10. THORACIC STERNITES: In males each thoracic sternite bears a tubercle.

11. ABDOMEN: Abdominal segments narrow with small bilobed epimera. A transverse groove dividing the sixth abdominal segment.

12. UROPODS: External branch broader than internal branch with two segments on external branch.

13. TELSON: Large, constricted near the base; two long keels present on dorsal surface; lateral margins armed with spines arranged in series of larger spines with smaller ones between; apex armed with two strong, curved spines connected at the base to form a backwardly directed crescent.

14. MARSUPIUM: Seven pairs of oostegites.

³ From Tattersall and Tattersall, 1951.
⁴ Compiled from Sars, 1885; Fage, 1941; and Tattersall and Tattersall, 1951.

KEY TO THE SPECIES OF THE GENUS *Gnathophausia*⁵

- a. Antennal scale small, not jointed, no strong rib terminating in a spine on outer margin; outer margin serrate. Epimera of sixth abdominal segment united ventrally, forming together a cordiform, concave plate, incised at apex. Dorsal keel of carapace interrupted. Lower lateral keel not curving upward behind, but terminating in a spine at the postero-inferior angle. Branchiostegal lobe generally with a well developed spine (sometimes obsolete). Maxillipeds with a small exopodite.
- b. Both lappets of the epimera of the second to fifth abdominal segments pointed and spiniform. Antennal scale subovate, apex shortly pointed. *ingens*
 - b'. Anterior lappet of the epimera of the first to the fifth abdominal segments small, rounded; posterior lappet pointed and spiniform. Antennal scale sublanceolate, tapering to a sharp spiniform point. *gigas*
- a'. Antennal scale large, of usual form, jointed at the extremity, outer margin formed by a strong rib terminating in a spine. Epimera of sixth abdominal segment not confluent ventrally.
- b. Lower lateral keel of carapace not curving up behind, but terminating in a spine on the postero-inferior angle of the carapace. Median keel of carapace interrupted, with spiniform serrations. Median line of abdominal segments with strong spines. Upper lateral keel of carapace wanting. Two epimeral spines on each side of the anterior section of the sixth abdominal segment. Maxillipeds with exopodite. *gracilis*
 - b'. Lower lateral keel of carapace curving up behind; no spine at postero-inferior angle of carapace. Median keel of carapace not interrupted, without spiniform serrations. Median line of abdominal segments—if armed at all—only with posteriorly projecting, small spines. Upper lateral keel of carapace present, very rarely wanting. Maxillipeds without exopodite.
 - c. Two epimeral spines on each side of anterior section of sixth abdominal segment. Upper lateral keel of carapace present. Antennal spine obsolete. Branchiostegal lobe with a well-marked triangular spine. Spine of outer margin of antennal scale projecting considerably beyond terminal lobe, serrated on both margins. . . . *longispina*
 - c'. One epimeral spine on each side of anterior section of sixth abdominal segment. Antennal spine more or less distinct. Branchiostegal lobe without spine, generally rounded, rarely angular. Spine of outer margin of antennal scale not, or only slightly, projecting beyond terminal lobe.
 - d. Upper lateral keel of carapace present.
 - e. Abdominal segments dorsally slightly keeled, with small, posteriorly projecting spines. Epimera of five anterior abdominal segments pointed posteriorly. Branchiostegal lobe rounded.
 - f. Carapace not suddenly constricted anteriorly and forming no shoulder. Branchiostegal lobes moderately developed. . . . *zoea*
 - f'. Carapace suddenly constricted anteriorly, forming a distinct shoulder in front of the anterior ends of the upper lateral keels. Branchiostegal lobe greatly expanded. *scapularis*
(or *zoea* var. *scapularis*)

⁵ Based on Ortmann, 1906, with alterations.

e'. Abdominal segments dorsally not keeled, without spines. Epimera of the five anterior abdominal segments rounded posteriorly. Branchiostegal lobe slightly angular. *affinis*

d'. Upper lateral keel of carapace wanting. Branchiostegal lobe rounded or angular, but without spine. Abdominal segments dorsally without keel, but posteriorly with a small, depressed triangular projection. Epimera of five anterior abdominal segments ending in small points posteriorly. *elegans*

SIZE AND SEXUAL MATURITY

Gnathophausia ingens (Dohrn 1870)
Figs. 3 and 4

- Gnathophausia calcarata* G. O. Sars, 1885
- " *bengalensis* Wood-Mason, 1891
- " *doryophora* Illig, 1906

A total of 204 specimens of *Gnathophausia ingens* were identified from the Scripps 1950-53 collections, consisting of 112 females, 23

males, and 69 juveniles, ranging in size from 25 mm to 139 mm body length (Table 1). The 15 largest specimens (all greater than 110 mm as measured from the level of the eyes to the end of the telson) are listed in Table 2. The body length is normally measured from the base of the rostrum at the level of the eyes to the end of the telson. However, in many cases in past literature, measurements are given which include the rostrum. This latter measurement of total length is less reliable because of dam-

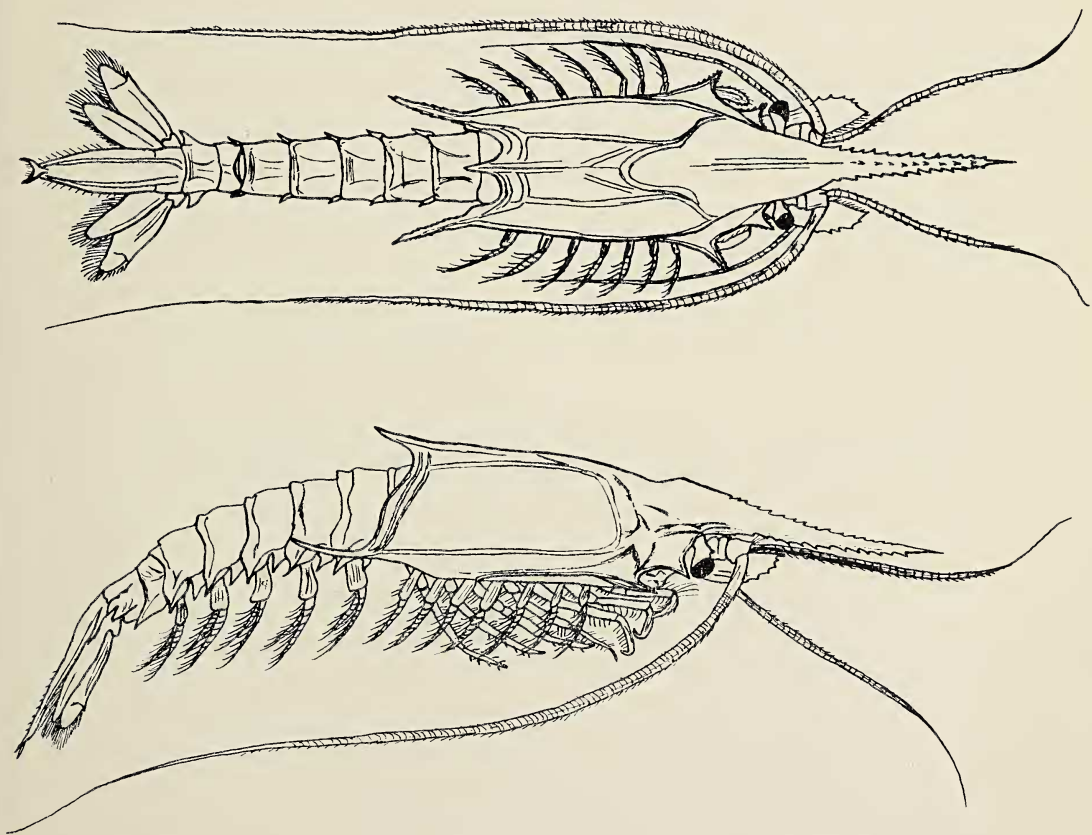


FIG. 3. *Gnathophausia ingens*, young specimen of 98 mm total length. (From Sars, 1885.)

TABLE 1 Continued

STATION	DATE	POSITION		DEPTH OF HAUL (meters)	BOTTOM DEPTH (meters)	TIME	NUMBER AND SIZE (mm) OF INDIVIDUALS								
		Latitude	Longitude				<i>Gnathoboaia ingens</i>			<i>Gnathoboaia gigas</i>			<i>Gnathoboaia gracilis</i>		
H52-338	6/ 7/52	00°17.7'– 00°42.0'N	110°26'– 110°12'W	1280	3823	0545–1145	Small <60	Medium 60–100	Large >100	Small <60	Medium 60–100	Large >100	Small <60	Medium 60–100	Large >100
H52-363	7/ 1/52	06°58'S– 06°48.5'S	88°35'– 88°30'W	1463	2195	0840–1439	—	—	—	—	—	—	1	—	—
H52-367	7/ 4/52	04°04'– 03°52'S	82°14'– 82°14'W	1641	3658	0450–1050	—	—	—	—	—	—	1	—	—
H52-404	8/ 8– 9/52	01°43'– 01°49'S	89°52'– 90°00'W	1016	2560– 2972	1944–0145	—	—	—	—	—	—	4	—	—
H52-409	8/11– 12/52	01°01.5'– 00°55.0'N	91°45.7'– 91°30.5'W	938– 1108	2286	1816–0017	—	—	—	—	—	—	1	—	—
					TOTALS		87	94	23	50	11	5	58	64	6
							204			66			128		

age or breakage to the rostrum which frequently occurs during sampling and preservation of the specimens.

The largest specimen of *G. ingens* on record is a giant female measuring 350 mm total length (from the tip of the rostrum to the end of the telson). This specimen was captured with the Isaacs-Kidd Midwater Trawl in 1955 on the Scripps Institution of Oceanography's Eastropic Expedition in the equatorial Pacific and was described by Clark (1961). This giant specimen is more than 1½ times larger than the previously reported largest specimen, a male from the Talisman Expedition (Hansen, 1927) with a body length of 185 mm (210 mm total length including the rostrum) which was taken in the Atlantic Ocean south of the Azores. None of the specimens from the 1950–53 Scripps collections in the eastern Pacific exceeded these lengths. The largest is a male of 139 mm body length (160 mm including the rostrum).

Of the 204 specimens of *G. ingens* examined from the 1950–53 Scripps collections, none of the 112 females possessed a completely developed brood pouch. Although many of the larger specimens possessed oostegites as long as or longer than the thoracic legs, none was completely developed to form a true marsupium containing eggs or embryos.

Only three previous accounts of sexually mature females of this species have been reported. One was described by G. O. Sars (1885) from the Challenger Expedition and measured 157 mm total length. A second, described by Fage (1941) from the Dana Expedition, measured 140 mm (165 mm including the rostrum). The oostegites on the latter specimen were clearly longer than the thoracic legs and measured 50 mm in length and 18 mm at their greatest width. The third was the giant female specimen described by Clark (1961).

The criterion used for the determination of sexual maturity in female mysids is the presence of a well developed marsupium. In the case of the males it is more difficult to recognize sexual maturity because of the difficulty in determining when the male genital pore, located on the last thoracic leg, is mature and functional.

The sizes 140 and 157 mm body length may be considered as the minimum sizes of sexual

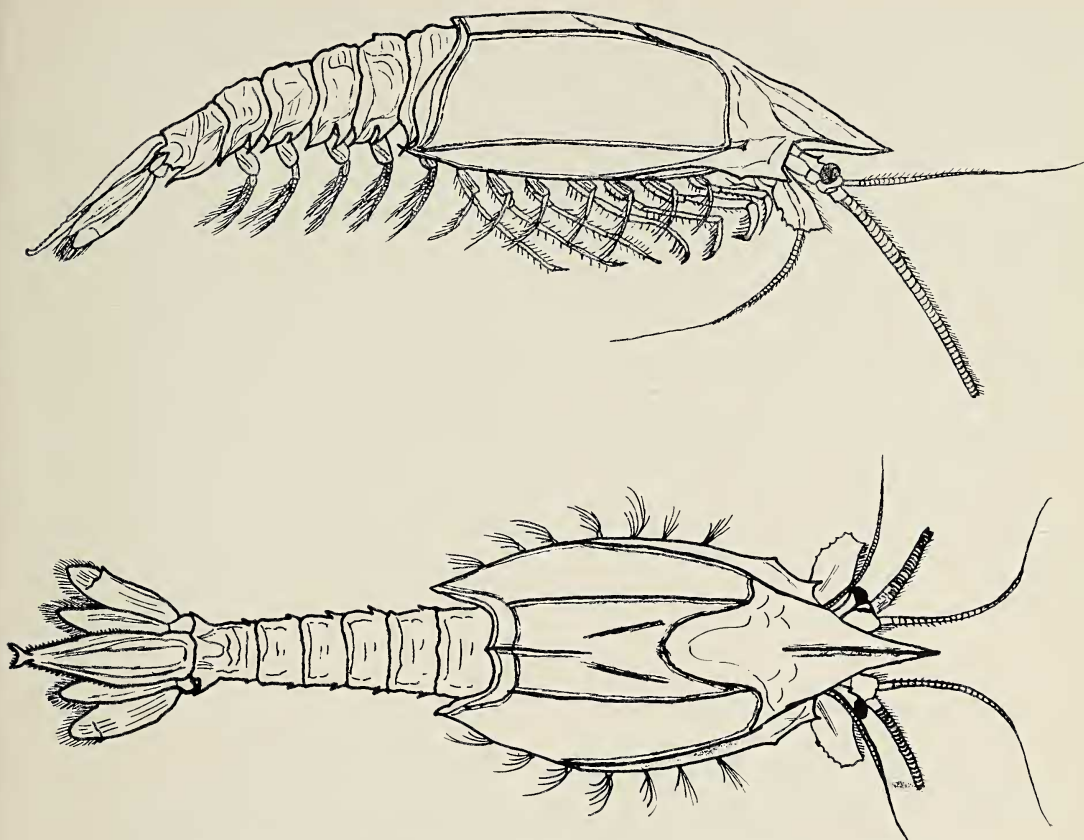


FIG. 4. *Gnathophausia ingens*, adult female of 157 mm. (From Sars, 1885.)

TABLE 2

Gnathophausia ingens

SIZE AND LOCATION OF LARGEST SPECIMENS CAPTURED

SIZE (mm)		SEX	STATION*	DEPTH OF HAUL (meters)	APPROXIMATE LOCATION*
Without Rostrum	Rostrum Included				
139	160	M	H51-85	549	off Baja California, Mex.
134	155	M	H52-309	1105	off Southern Mexico
125	143	F	H51-162	914	off Baja California, Mex.
123	144	F	H52-32	732	off San Diego, Calif.
123	144	F	H52-15	?	off San Diego, Calif.
122	?	F	H51-162	914	off Baja California, Mex.
120	138	F	H50-277	732	off San Diego, Calif.
118	137	F	H51-90	2213	off Baja California, Mex.
115	138	F	H50-277	732	off San Diego, Calif.
115	134	F	H50-269	750	off San Diego, Calif.
114	135	F	H52-309	1105	off Southern Mexico
114	134	F	H51-85	549	off Baja California, Mex.
113	136	F	H51-45	799	off San Diego, Calif.
113	133	F	H51-45	799	off San Diego, Calif.
111	130	F	H50-277	732	off San Diego, Calif.

* See Table 1 for exact locations.

maturity in the case of the female *G. ingens*. Fage (1941) reports another female from the Dana Expedition, larger than his sexually mature female of 140 mm, measuring 142 mm (168 mm with the rostrum), in which the oostegites were only 20 mm long and 5 mm wide, i.e., not yet fully formed. Thus there seems to be a range for the size at which sexual maturity occurs in *G. ingens* with some individuals maturing at a smaller size than others.

Gnathophausia gigas Willemoes-Suhm, 1875
Fig. 5

Gnathophausia drepanophora Holt and
Tattersall, 1905

A total of 66 specimens of *Gnathophausia gigas* were identified from the 1950-53 Scripps collections: 10 females, 9 males, and 47 juveniles, ranging in size from 21 to 142 mm body

length. Table 3 presents information about the 5 specimens of *G. gigas* greater than 100 mm in body length.

The male of 164 mm total length (142 mm body length) from Station H51-355 is slightly larger than the previously reported largest specimen, a female of 160 mm total length (Tattersall, 1914). The next largest previously reported specimens were 2 females of 135 mm and 133 mm total length described by Nouvel (1943).

A single female measuring 105 mm body length from Station H51-366 possessed brood lamellae which were well developed into a completely formed brood pouch. The marsupium was empty, however, the embryos evidently having been recently discharged. The brood lamellae measured 27 mm in length and 8 mm at their greatest width. This mature female specimen was captured at a depth of 2972 m over a bottom depth of 3658 m. It has been

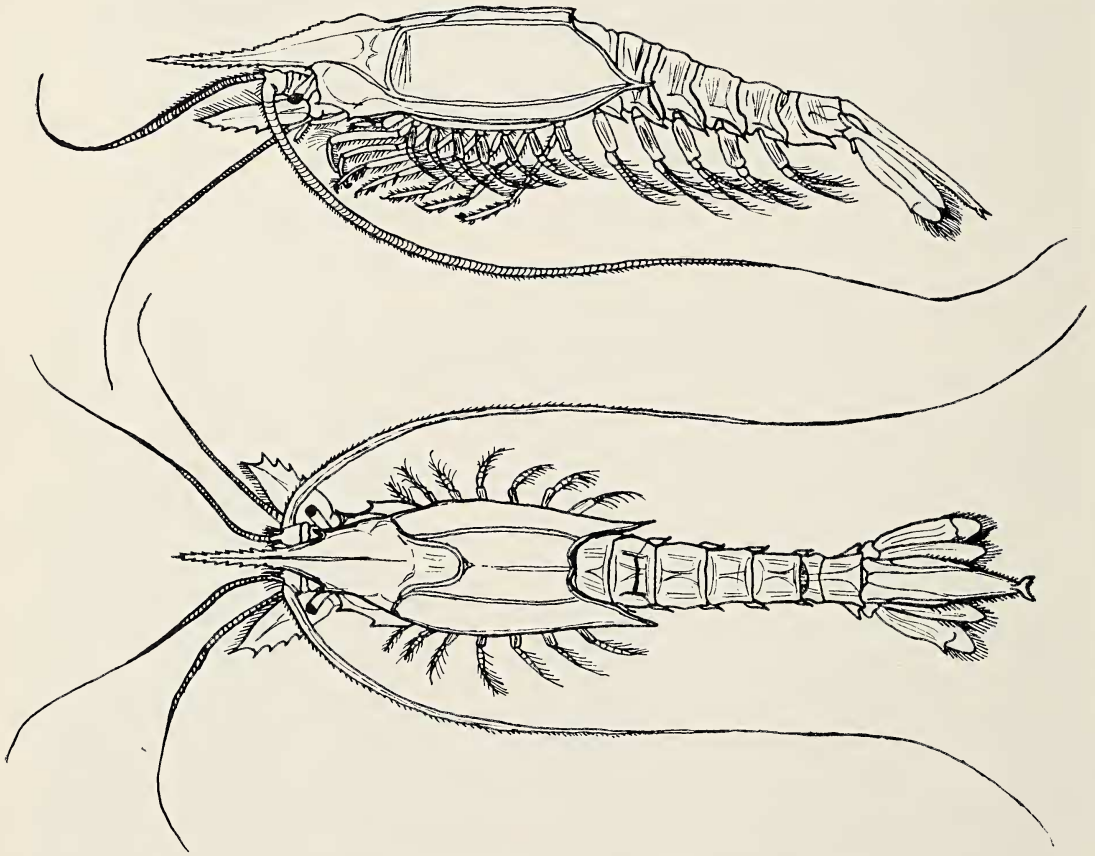


FIG. 5. *Gnathophausia gigas*, adult male of 142 mm. (From Sars, 1885.)

postulated by some that this species and possibly other species of *Gnathophausia* approach the bottom at sexual maturity, thus accounting for the difficulty in obtaining mature specimens with the traditional pelagic nets. It appears, however, that this mature specimen was not near the bottom, having been taken at least 600 m from the bottom when captured with the midwater trawl during the early hours of the morning (from 0300 to 0831 hours).

The minimum size for sexual maturity in this species is probably around 120 mm total length. Ortmann (1906) reports a female of 119 mm total length with fully developed oostegites forming a marsupial pouch. This is the smallest known sexually mature female of this species. On the other hand, the large female of 145 mm total length from the Scripps collections did not possess a fully developed marsupium. Apparently there is a range of size at which sexual maturity occurs, and it is a wide range in this species.

Gnathophausia gracilis Willemoes-Suhm, 1875

Fig. 6

Gnathophausia brevispinis Wood-Mason,

1891.—Faxon, 1895

" *dentata* Faxon, 1893

" *bidentata* Illig, 1906

A total of 128 specimens of *Gnathophausia gracilis* were identified from the Scripps 1950–53 collections: 64 females, 27 males, and 37 juveniles, ranging in size from 22 mm to 115 mm body length. Table 4 lists the individuals

greater than 100 mm in body length. All 6 of these specimens are larger than the largest ones reported in previous literature. The nearly 250 specimens of *G. gracilis* gathered on the Dana Expedition and reported by Fage (1941) range in size from 20 mm to 100 mm. The 3 largest Dana specimens (2 males and 1 female, each measuring 100 mm in body length) all came from the western Atlantic Ocean in the vicinity of the Caribbean Sea.

The single specimen from the Challenger Expedition described by Sars (1885) measured 41 mm total length (including rostrum). The 2 specimens from the Gulf of Bengal studied by Wood-Mason (1891) were immature and measured 83 mm and 92 mm total length. The John Murray Expedition collected 8 specimens from 22 to 78 mm in length. The Discovery Reports (Tattersall, 1955) list 3 specimens from 24 to 58 mm in size.

Fage (1941) states that the size at which *G. gracilis* reaches sexual maturity is greater in the Atlantic and Indian Oceans than in the Pacific; in the latter, especially the eastern Pacific, there exists a relatively dwarf form of *G. gracilis*. He cites a small female of 52 mm taken in the Gulf of Panama on the Dana Expedition with a completely developed marsupium containing embryos. Fage indicates that there is no evidence that the adults of *G. gracilis* abandon their pelagic life in order to approach the bottom at the time of sexual maturity, and he shows that completely adult females were numerous at all levels in the pelagic fishings of the Dana. The smallest female adult

TABLE 3

Gnathophausia gigas

SIZE AND LOCATION OF LARGEST SPECIMENS CAPTURED

LENGTH (mm)		SEX	STATION*	DEPTH OF CAPTURE (meters)	APPROXIMATE LOCATION*
Without Rostrum	Rostrum Included				
142	164	M	H51-355	3400	off Northern Calif.
126	145	F	H51-161	2085	off Baja California, Mex.
110	?	F	H51-90	2213	off Baja California, Mex.
105	127	F	H51-366	2972	off Alaska
102	125	M	H51-371	4023-4389	off British Columbia

* See Table 1 for exact locations.

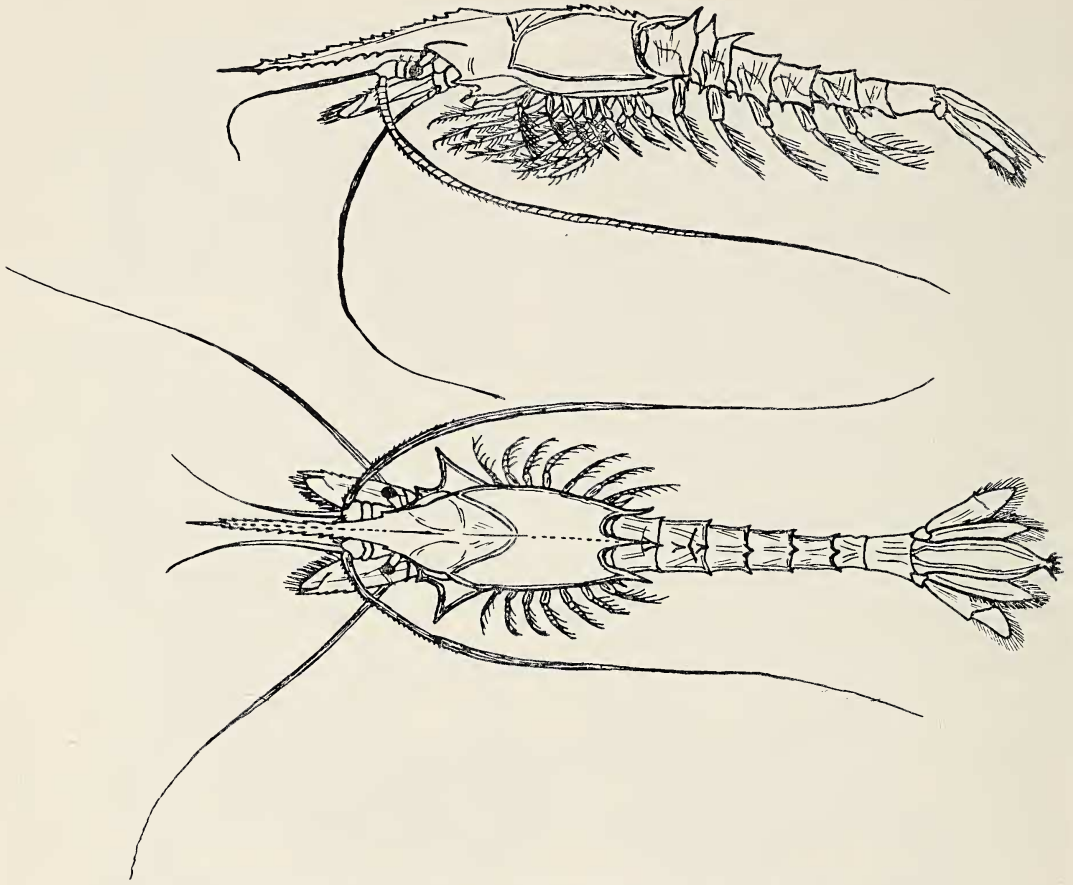


FIG. 6. *Gnathophausia gracilis*, young male specimen of 41 mm. (From Sars, 1885.)

with a completely formed brood pouch taken by the Dana also comes from the Gulf of Panama and measures 49 mm body length. Fage also points out that females of this size from the Caribbean Sea have only rudimentary oostegites and reach their sexual maturity at a larger size. The large female specimen taken from the Gulf of Bengal (Wood-Mason, 1891), measuring 92 mm total length, had incompletely developed brood lamellae which measured only 3 mm in length.

None of the 5 large females of greater than 100 mm body length from the Scripps collections possessed a completely formed brood pouch.

Gnathophausia zoea Willemoes-Suhm, 1875

Gnathophausia Willemoesi G. O. Sars 1885

" *Sarsi* Wood-Mason, 1891

" *crinata* Illig 1906

Only 2 specimens of *Gnathophausia zoea* (1 male and 1 female) were found in the Scripps 1950-53 collections. Both were taken at Station H52-404, located just south of the equator at $1^{\circ}43'S$, $89^{\circ}52'W$ to $1^{\circ}49'S$, $90^{\circ}00'W$. The depth of the haul was 1016 m, over a bottom depth of 2560 to 2972 m. In addition 4 other specimens of *Gnathophausia* (all *G. gracilis*) were taken at this station, which was occupied during the time interval from 0144 to 0145 hours on August 8-9, 1952. The female *G. zoea* measured 48 mm body length (approximately 70 mm including the rostrum). The male measured 41 mm body length (67 mm with the rostrum). This species is rarely taken off the west coast of North America.

Gnathophausia zoea has a wide horizontal distribution, occurring from the Arctic Circle to the Equator. It is especially widespread in

the Atlantic Ocean and in the area of Indonesia in the South Pacific. Fage (1941) has contrasted its wide distribution in the Atlantic with its localization in the tropical zone in the Pacific.

Fage also points out that this species is less strictly bound to the great depths, occurring in a wide range of depths (from 200 m to 3000 m in the captures of the Dana Expedition). The 2 specimens from the Scripps collections came from approximately 1000 m.

HORIZONTAL DISTRIBUTION

The Scripps 1950–53 collections studied here were obtained from the eastern Pacific Ocean within an area extending to 160°W and between 60°N and 10°S. Figure 7 shows the locations of captures of the three species of *Gnathophausia* predominant in the collections.

The more northerly species in the eastern Pacific is *G. gigas*, occurring mainly north of 30°N. South of 40°N *G. ingens* takes over, ranging south to approximately 20°N. Below 20°N there is only one station (Station H52–309) where *G. ingens* was identified from the Scripps collections, with the exception of the "giant" specimen of *G. ingens* described by Clark (1961), which was captured in 1955 between 7°50'N, 120°13'W and 8°12'N, 119°54'W.

G. gracilis overlaps the distribution of *G. ingens* between 20°–40°N and is the predominantly tropical form occurring in equatorial samples where neither of the other two species was found.

Gnathophausia ingens

The worldwide occurrence of *G. ingens* falls generally between 40°N and 40°S. Within these limits we find some interesting variations in distribution in different portions of the world's oceans.

Figure 8 shows that *G. ingens*, although scarce in equatorial waters of the eastern Pacific Ocean, is abundant in equatorial waters in other oceans. Fage (1941) comments on the rarity of this species east of the Samoan Islands in the eastern Pacific Ocean, as indicated by the captures of the Dana and previous expeditions. He speculates on the low oxygen tension in this area in the deep-water habitat of the species as being responsible for this lack of specimens. On the contrary, I have found that, off the coasts of California and Baja California, between 20°–40°N, *G. ingens* is the most abundant species of *Gnathophausia* in the Scripps collections taken from this portion of the eastern Pacific. It is more than twice as abundant in our captures from this region as is *G. gracilis*, and 18 times as numerous as *G. gigas*. *G. ingens* is, however, notably absent from our stations occupied in the equatorial zone where *G. gracilis* is the dominant species (Fig. 7). Whether *G. ingens* again becomes more abundant between 15° and 40°S in the eastern Pacific is only speculation until samples can be studied from collections made in these areas. The samples studied here did not extend beyond 8°S (Station H52–363).

Possibly temperature is a factor in this dis-

TABLE 4

Gnathophausia gracilis

SIZE AND LOCATION OF LARGEST SPECIMENS CAPTURED

SIZE (mm)		SEX	STATION*	DEPTH OF HAUL (meters)	APPROXIMATE LOCATION*
Without Rostrum	Rostrum Included				
115	136	F	H51–84	914	off Baja California, Mex.
113	138	F	H51–77	1810	off Baja California, Mex.
113	134	M	H51–90	2213	off Baja California, Mex.
106	120	F	H51–77	1810	off Baja California, Mex.
105	?	F	H51–91	2012	off Baja California, Mex.
103	122	F	H51–90	2213	off Baja California, Mex.

* See Table 1 for exact locations.

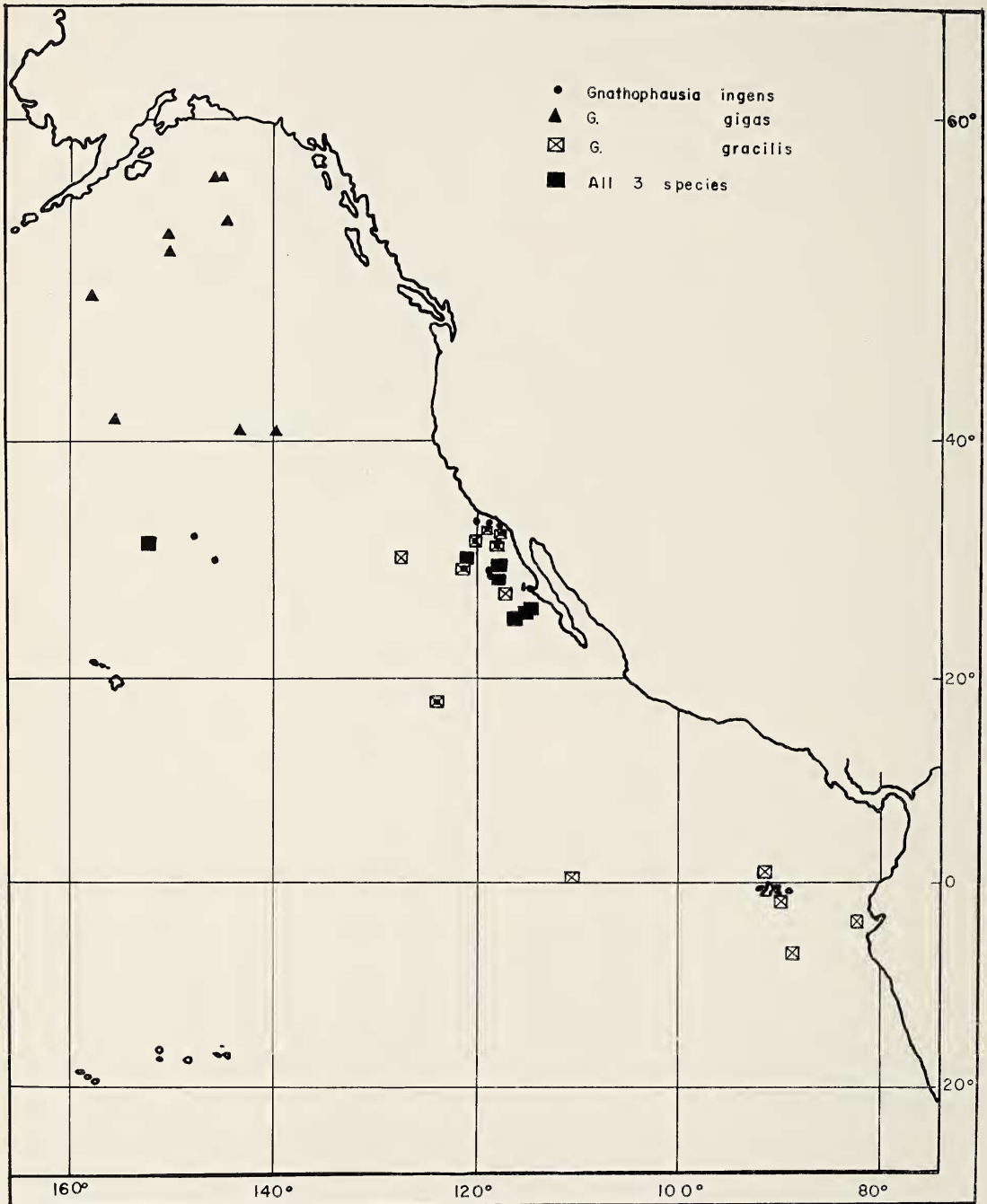


FIG. 7. Locations of captures of the three predominant species of *Gnathophausia* from the Scripps 1950-53 collections in the eastern Pacific Ocean.

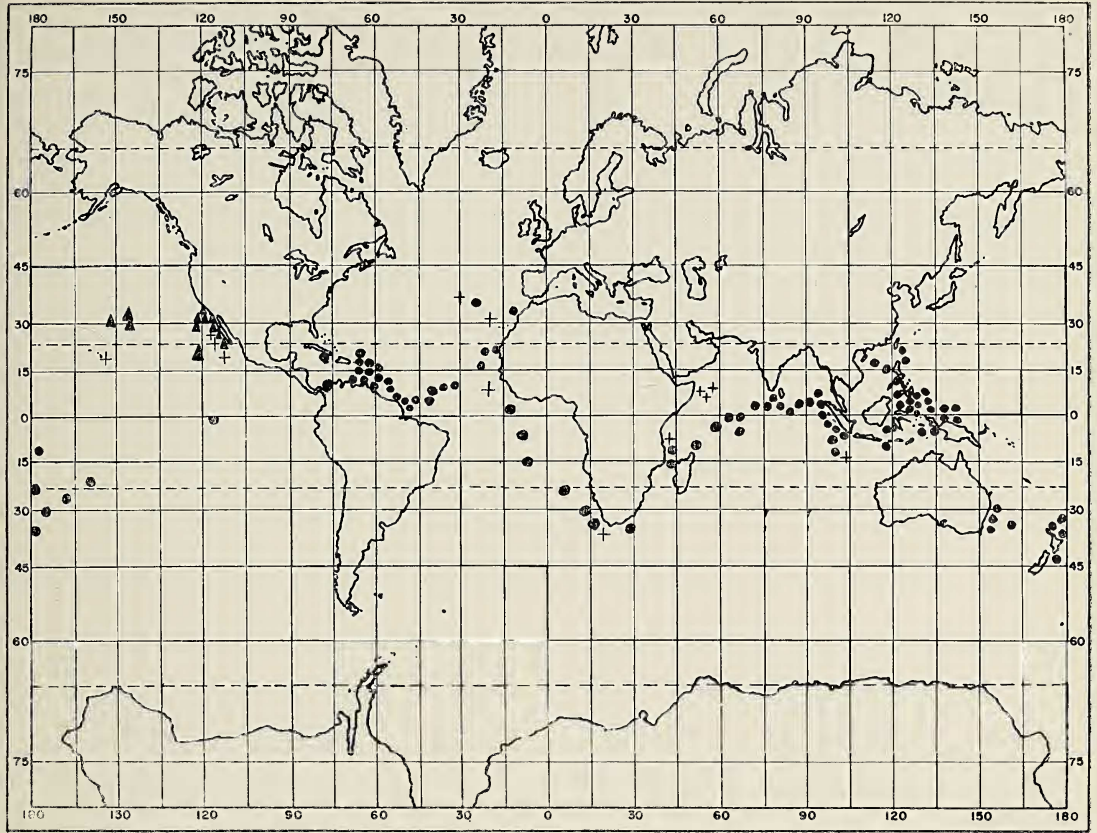


FIG. 8. Geographical Distribution of *Gnathophausia ingens*. Solid circle, captures of the Dana Expedition; plus sign, other previous captures; solid triangle, captures from the 1950-53 Scripps collections.

tribution between 15°N and 40°N in the eastern Pacific, but Figure 8 shows that the distribution of *G. ingens* in the other oceans (especially in the Atlantic) and in other portions of the Pacific is not restricted to these latitudes. In the western Pacific and in the Indian Ocean this species is frequently found in the equatorial zones.

Figure 8 further shows that *G. ingens* occurs at mid-latitudes (between 20°-40°N) and is rare in the lower latitudes in the eastern portions of both the Atlantic and Pacific oceans. And, conversely, the species is more abundant in the lower latitudes and rare in mid- and higher latitudes in the western portions of both oceans. Fage (1941) correlates this strange distribution in the Atlantic with temperature isotherms at 600 m. He has shown that the distribution of *G. ingens* falls within the zone of

temperatures of less than 10°C, and is excluded from areas of temperatures of greater than 10°C.

Gnathophausia gigas

The wide latitudinal range of *G. gigas* is shown in Figure 9. This species is found from near the Equator to nearly 60°N in both the Atlantic and Pacific oceans. In the Southern Hemisphere *G. gigas* has been found as far south as 69°S in the Indian Ocean (Tattersall, 1955). In the Scripps 1950-53 collections *G. gigas* was the only species of this genus which was taken north of 35°N in the eastern Pacific, having been found as far north as nearly 60°N. Fage (1941) suggests that this animal prefers the colder waters, and there is evidence that *G. gigas* lives deeper in the oceans where the

superficial waters are warmer and lives in shallower water when these waters are colder, apparently seeking out temperatures in the 4°C isotherm region.

Gnathophausia gracilis

This species, by contrast, is confined to a small latitudinal range between 35°N and 20°S (Fig. 10). Previously only four captures had been made outside the tropical zone (i.e., 23°N to 23°S), these being taken from the Atlantic Ocean. None had been taken north of the Tropic of Cancer in the Pacific. However, of the 128 individuals of *G. gracilis* in the Scripps collections, a total of 99 specimens were found from stations north of the Tropic of Cancer. A great majority of the larger individuals (greater than 80 mm body length) came from north of the Tropic of Cancer, and all of the largest in-

dividuals of greater than 100 mm body length came from north of 23°N, the maximum latitude of occurrence being 33°N. However, compared with the other species of *Gnathophausia*, *G. gracilis* was the most conspicuous species in the Scripps hauls from the tropical regions of the eastern Pacific, with no *G. gigas* and only a few *G. ingens* occurring in collections taken south of the Tropic of Cancer.

Fage (1941) reports that the *G. gracilis* found in the Pacific (especially in the eastern Pacific where, in the Gulf of Panama, the adults captured by the Dana did not exceed 65 mm length) are of smaller size than those of the Atlantic. His largest specimens (2 males and 1 female, each 100 mm in length) came from the Atlantic in the vicinity of the Caribbean Sea, and he believes that sexual maturity is more precocious in the specimens from the Pacific, particularly in the eastern Pacific, where



FIG. 9. Geographical Distribution of *Gnathophausia gigas*. Solid circle, captures of the Dana Expedition; plus sign, other previous captures; solid triangle, captures from the 1950-53 Scripps collections.

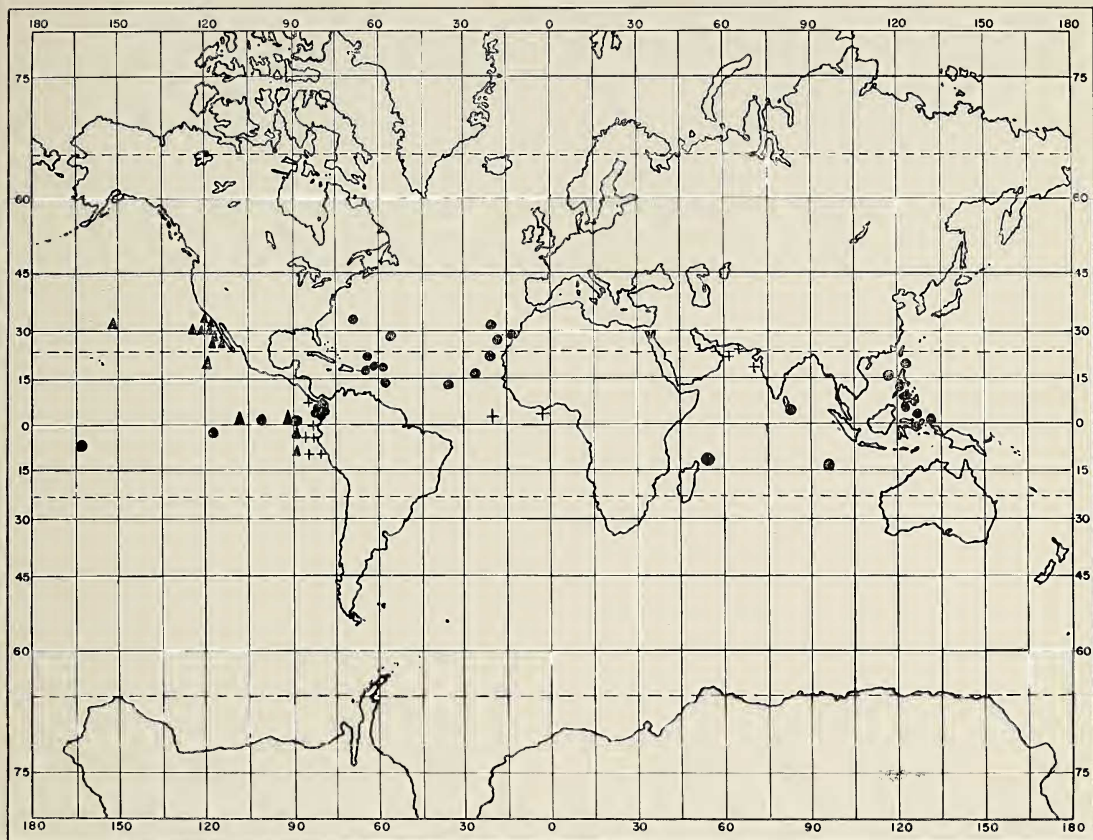


FIG. 10. Geographical Distribution of *Gnathophausia gracilis*. Solid circle, captures of the Dana Expedition; plus sign, other previous captures; solid triangle, captures from the 1950-53 Scripps collections.

TABLE 5

DISTRIBUTION OF *Gnathophausia gracilis* ACCORDING TO SIZE IN ATLANTIC AND PACIFIC OCEANS (FROM FAGE, 1941)

NUMBER OF INDIVIDUALS	LENGTH (mm)	ATLANTIC		PACIFIC	
		East	West	East	West
79	50-70	5.0%	2.5%	58.2%	34.2%
14	71-100	7.1%	57.1%	0	35.7%

he found all the adults to be of relatively small size, as shown in Table 5.

Table 6 similarly illustrates the numbers and percentages of the various sized individuals in the Scripps collections taken from two portions of the eastern Pacific: (1) north of 23°N (where Fage lists no captures from the Dana), and

(2) south of 23°N. Thus it can be seen that of the specimens coming from south of the Tropic of Cancer, the majority (75.9%) are less than 80 mm in length (without the rostrum). This percentage actually refers to specimens under 60 mm in length, since no specimens between 61 and 80 mm were found in samples from this southern region in the Scripps collections. From the area north of the Tropic of Cancer the majority of the specimens taken (59.6%) were of the larger size, i.e., greater than 80 mm. Apparently the size difference noted by Fage would not apply to the entire eastern Pacific, but only to that portion within the tropical zone, and particularly in the area of the Gulf of Panama where, indeed, a dwarf form does seem to exist, which reaches sexual maturity at half the size of the normal adult *G. gracilis*.

TABLE 6

DISTRIBUTION OF *Gnathophausia gracilis* IN EASTERN PACIFIC ACCORDING TO SIZE

EASTERN PACIFIC NORTH OF TROPIC OF CANCER			EASTERN PACIFIC SOUTH OF TROPIC OF CANCER		
Number of Individuals	Length (mm)	Percentage	Number of Individuals	Length (mm)	Percentage
58	<80	59.6	22	<80	75.9
41	81-115	41.4	7	81-115	24.1
Total 99			Total 29		

VERTICAL DISTRIBUTION

The Isaacs-Kidd Midwater Trawl is not equipped with a closing device, so that the exact depth of capture cannot be determined for specimens collected with this sampler. The maximum depth, however, is used as the assumed depth of capture, while recognizing that, although the majority of specimens were most likely captured at the maximum depth where the greatest length of trawling time is spent, there is still the possibility of catching stragglers between this depth and the surface as the net is raised. All depths of capture referred to in this paper have been calculated by measuring the amount of wire played out, then correcting for the wire angle to compute the actual collecting depth of the trawl.

Of the three predominant species of *Gnathophausia* found in the Scripps collections from the eastern Pacific, *G. gigas* is the deepest-occurring (average depth of capture, 2100 m). Another somewhat less deeply-occurring species is *G. gracilis*, with an average depth of capture in the Scripps collections of 1600 m. *G. ingens* occurs predominantly in more shallow waters, where its average depth of capture was 1100 m. A weighted average depth of capture for *G. ingens* was also calculated, taking into consideration the number of specimens captured at each depth. This weighted average depth of 850 m shows that the majority of specimens of *G. ingens* were found at an even more shallow average depth.

Time-depth graphs have been plotted for the three predominant species of *Gnathophausia* found in the 1950-53 Scripps collections (Figs. 11, 12, and 13), in order to detect any possible evidence of nocturnal vertical migrations.

In only one species, *G. ingens*, is there any evidence that the animals are found, in general, in more shallow water during night collections and in deeper water during daytime collections. The graph shows that during the day practically no specimens of *G. ingens* were taken above 650-700 m. On the other hand, the majority of captures at night recovered individuals from the zone between 274 and 650 m. All captures at night from deeper than 650-700 m were from hauls which extended into the daylight period; thus there is the possibility that the specimens were picked up at these deeper levels during the daylight period of towing.

Similar time-depth graphs for *G. gigas* and *G. gracilis* do not seem to indicate any consistent depth differences between daylight and dark sampling. In order to study more precisely the possible existence of nocturnal vertical migration in *Gnathophausia* it would be necessary to employ the use of closing nets to determine more accurately the exact depths of capture. For even more accurate determinations a depth telerecording unit has been employed (Boden et al., 1955).

Gnathophausia gigas

Although *G. gigas* tends to occur at greater depths than the other two species, it was occasionally collected in more shallow water (less than 1000 m) than that which Fage (1941) reports as the shallowest depth of occurrence of this species for the captures of the Dana (2000 m depth, 3000 m of wire out). The average depth of capture of *G. gigas* in the Scripps collections was 2100 m, ranging from 600 to 4400 m. Only 3 (19%) of the 16 stations where *G. gigas* occurred were at less than

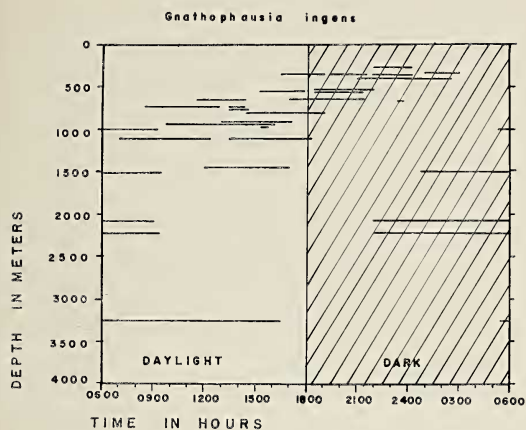


FIG. 11. Captures of *Gnathophausia ingens* plotted according to depth of haul and time of day.

1000 m. This involves 8 individuals (12%) in the total of 66 individuals of this species examined. This compares with 20 of the 34 stations for *G. ingens* (59%) which were at less than 1000 m, and with 5 of the 22 stations (23%) for *G. gracilis*. All specimens of *G. gigas* in the Scripps collections of greater than 100 mm body length came from depths of more than 2000 m.

Closing nets used on the Discovery Expedition (Tattersall, 1955) found immature *G. gigas* at between 650–4000 m depth. Banner (1947) reports on 9 specimens of *G. gigas* from the eastern Pacific off Canada at between 400–1200 m depth, and 15 specimens off Alaska from depths of 300–900 m. These specimens were all smaller than 60 mm body length.

Gnathophausia gracilis

G. gracilis has always been described as a species from very deep water (greater than 1500 m). Previous reports show that all records of *G. gracilis* were from depths greater than 1500 m, except for 2 young specimens described by Fage (1941) and Hansen (1927), which were from 800 m. The Scripps collections yielded 30 individuals (collected at 5 separate stations) from depths of less than 1000 m, some of them greater than 100 mm in size.

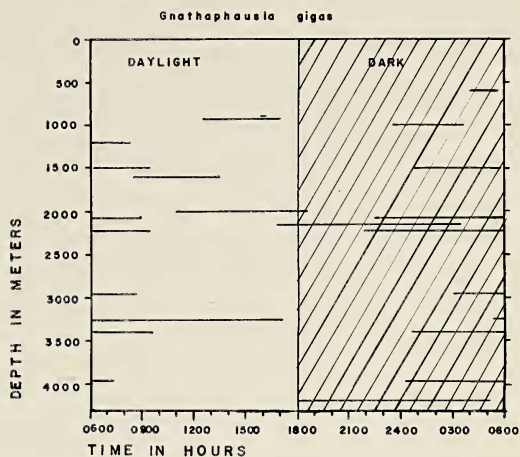


FIG. 12. Captures of *Gnathophausia gigas* plotted according to depth of haul and time of day.

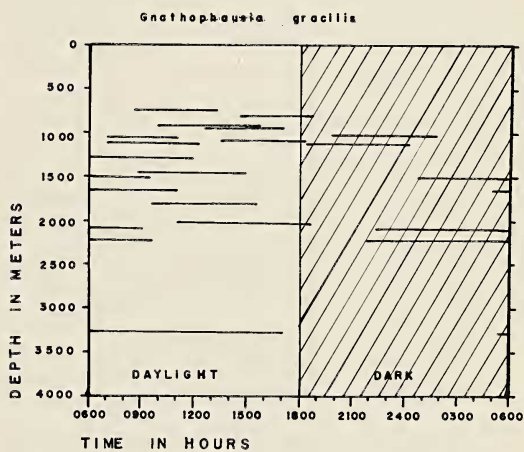


FIG. 13. Captures of *Gnathophausia gracilis* plotted according to depth of haul and time of day.

This amounts to 23% of the total of 128 individuals of this species examined in the Scripps collections. The 2 most shallow depths sampled yielding *G. gracilis* were 732 m (Sta. H50-277), with 1 small male, and 799 m (Sta. H51-45), with 6 juveniles and 3 males. The average depth of capture from the Scripps collections was 1600 m, ranging from 732 to 3914 m.

Fage (1941) suggested that *G. gracilis* maintains itself at a deeper level in the eastern por-

tions of the Atlantic and Pacific oceans than in the western portions mainly in order to escape the zone of low oxygen content. Having studied the temperature, salinity, and oxygen content, he found that in the eastern portions the waters are colder, less saline, and poorer in oxygen content than at the same level in the western portions. Fage listed depths of between 1500 to 2000 m as the zone where *G. gracilis* normally lives. He pointed out that *G. gracilis* is a true bathypelagic species and not a form which lives on the bottom, as was previously believed. A study of Table 1, where the depth of haul and the bottom depth are given for the Scripps collections, also shows this to be true. In all stations where *G. gracilis* was found the depth of capture is from 400 to 2600 m from the bottom. The average difference between the depth of capture and the bottom depth for all positive stations of *G. gracilis* is 1512 m, a considerable distance from the bottom.

Gnathophausia ingens

G. ingens, in contrast to the other two species, occurs in greatest numbers above 1000 m. The average depth of capture in the Scripps 1950-53 collections was 1100 m, ranging from 274 to 3914 m. The majority of specimens were found at an average depth of 850 m (weighted average). Closing nets on the Discovery Expedition (Tattersall, 1955) show that *G. ingens* was most common between 600 and 1500 m, but was also found as deep as 2480-2580 m and as shallow as 210-340 m.

Previous studies have shown that the younger individuals of this species (less than 80 mm in length) are found at more shallow levels than are the larger, sexually mature adults. This is also generally true of the specimens from the Scripps collections. Fage (1941) has found that the peculiarities in vertical distribution, i.e., in certain areas of the Indian Ocean where young individuals were captured at considerably greater depths, can be explained by the vertical distribution of temperatures in those regions. He has found that the depth of occurrence of young individuals of less than 80 mm

length corresponds to depths where the 5°-8°C temperature range occurs. When this temperature occurs deeper, the young individuals occur deeper. He also states that in all the oceans no individual of a size greater than 80 mm has been taken with less than 1000 m of cable immersed, equivalent to an actual depth of 500-600 m. This is generally true of the 1950-53 Scripps collections, with the exception of 2 specimens of 81 and 87 mm body length from Stations H51-75 and H51-76, both taken at a depth of 366 m.

Although only 2 (or 8.7%) of the 23 individuals of *G. ingens* of greater than 100 mm size were taken at less than 600 m (Sta. H51-85), 17 (or 74.9%) of the specimens were from depths less than 1000 m (Table 2).

Fage (1941) states that individuals of *G. ingens* exceeding 80 mm in length are very rare and account for 18% among the captures of the Dana in the Atlantic, for 13% in the Indian Ocean, and only 7% in the Pacific. From the Scripps collections in the eastern Pacific I have found that 26.5% of the individuals were greater than 80 mm in body length. This increase over Fage's figures serves to point out the improved sampling ability of the midwater trawl in deep waters over traditional pelagic nets. Larger and faster swimming specimens are less able to evade capture or to swim out of the nets, due to the greater speed and efficiency of the midwater trawl.

PARASITES

Fage (1936, 1940, and 1941) has described a curious protozoan parasite, *Amallocystis fasciatus* (an ellobiopsid flagellate), which occurs occasionally in specimens of *Gnathophausia* (Fig. 14). Of the 1,051 specimens examined from the Dana Expedition, 5 individuals were found which contained this parasite: 3 *G. zoea* and 2 *G. ingens*.

Of the 400 individuals of the genus *Gnathophausia* which I examined from the Scripps collections, I found only 3 parasitized specimens: 2 *G. ingens* and 1 *G. gracilis*. No previous record of parasitism by this flagellate has been reported in *G. gracilis*. This parasit-

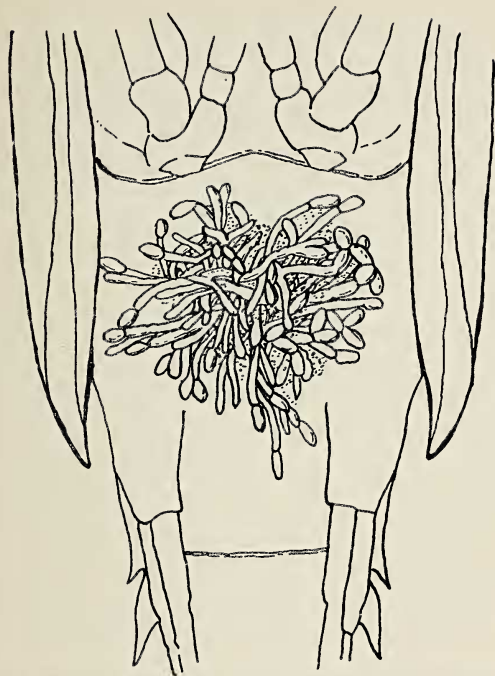


FIG. 14. First abdominal sternite of *Gnathophausia zoea* parasitized by *Amallocystis fasciatus*. (From Fage, 1941.)

ized *G. gracilis* is a female of 70 mm body length (87 mm including the rostrum) and was taken at Station H51-406 at a depth of 0-2926 m. Both parasitized *G. ingens* specimens are females, one of which came from Station H51-406 (from the same haul which captured the parasitized *G. gracilis*) at a depth of 0-2926 m and measured 86 mm body length (102 mm including the rostrum). The other parasitized *G. ingens*, a smaller female measuring 66 mm (82 mm including the rostrum), was taken at Station H52-15, the depth of capture being unknown over a bottom depth of 1207 m. In each case the parasite was attached to the middle of the ventral aspect of the first abdominal segment. Indeed, Fage describes this exact location as being constant among the 5 parasitized individuals which he examined from the collections of the Dana.

Nouvel (1941) also reports on 4 similarly parasitized individuals from the following three species of *Gnathophausia*: (1) *G. ingens*—1 parasitized specimen (a male of 110 mm measured from the antennal scale to the end of the

telson) from the eastern Atlantic off Mogador, Morocco, 0-4000 m; (2) *G. gigas*—1 parasitized female of 115 mm from the Atlantic Ocean south of Spain, 0-4740 m; (3) *G. zoea*—2 parasitized females of 45 and 39 mm from two locations in the eastern Atlantic off Portugal, one at 1241 m, the other at 0-1500 m.

Fage pointed out that the plate of fixation of this parasite is located just under the first abdominal nerve ganglion; and he observed a reaction of the host in the form of a great hypertrophy of this first abdominal ganglion as compared with the other abdominal and thoracic ganglia and with ganglia in normal, non-parasitized individuals.

Another influence of the parasite upon infected females is a retarded development of the secondary sexual characteristics, particularly the oostegites, which were considerably smaller and less well developed in the parasitized females than in non-infected females of the same size and presumably, of the same age. In addition, Nouvel describes an effect on the male *G. ingens*. In this male the sexual orifice is at the base of the last thoracic appendages. In addition this specimen has some very small outlines of oostegites at the bases of all the thoracic appendages except the last pair. This has been described as a "feminizing action" which the parasite exercises on the host.

In the 2 parasitized females of *G. ingens* from the Scripps collections, a retarded development in the oostegites was noted as compared with the normal, non-parasitized females. In both the 66 mm specimen and the 86 mm specimen the oostegites were extremely minute, less than 1 mm in length. A normal female of only 70 mm was found to have oostegites 2 mm in length, and a non-parasitized female of 80 mm possessed oostegites measuring 3 mm.

However, in the case of the parasitized *G. gracilis* of 65 mm which I examined, the oostegites measured 4 mm in length and 1 mm in width. These measurements are similar to those for normal, non-parasitized females of this species of approximately the same length. Thus the parasite does not seem to have retarded the development of the oostegites in this parasitized *G. gracilis*, in contrast to its effects on the other species of *Gnathophausia*.

SUMMARY

1. A total of 400 specimens of *Gnathophausia* were studied from the Scripps Institution of Oceanography's 1950-53 collections made with the Isaacs-Kidd Midwater Trawl, in the eastern Pacific Ocean, and four species were identified: (a) *G. ingens*: 204 specimens ranging in size from 25 to 139 mm body length (not including the rostrum), taken from a depth range of 274-3914 m, with an average depth of capture of 1100 m; (b) *G. gigas*: 66 specimens ranging in size from 21 to 142 mm body length, taken from a depth range of 603-4883 m, with an average depth of capture of 2100 m; (c) *G. gracilis*: 128 specimens ranging in size from 22 to 115 mm body length, taken from a depth range of 732-3914 m, with an average depth of capture of 1600 m; (d) *G. zoea*: 2 specimens, a female of 48 mm body length and a male of 41 mm body length, taken from a depth of 0-1016 m.

2. The geographical distribution of *G. gigas*, a colder water form, in the eastern Pacific is more northerly (20°-60°N) than is that of *G. ingens* and *G. gracilis*, which occur in warmer waters and exhibit a more tropical distribution, particularly *G. gracilis*.

3. Of the 128 specimens of *G. gracilis* collected 99 were found north of the Tropic of Cancer in the eastern Pacific Ocean, an area where they had rarely been found previously.

4. *G. ingens* was found consistently deeper in daylight hauls than in hauls taken at night, possible evidence for nocturnal vertical migration in this species. No evidence for this phenomenon is shown for *G. gigas* or *G. gracilis*.

5. Among the specimens of *G. gracilis* 6 were greater than 100 mm in body length, the largest measuring 115 mm. All are larger than any *G. gracilis* individuals previously described.

6. A mature female specimen of *G. gigas* measuring 105 mm in body length and having a well developed marsupium is described.

7. A parasitic ellobiopsis flagellate, *Amallocystis fasciatus*, is reported from 2 specimens of *G. ingens* and 1 specimen of *G. gracilis* taken from the eastern Pacific Ocean.

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